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Cover: *Saproamanita praeclara*: Sporocarp in habitat © Kantharaja. R.



## Hatching in Coromandel Marsh Dart Damselfly *Ceriagrion coromandelianum* (Fabricius) (Zygoptera: Coenagrionidae): process and influence of the oviposition substrate

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**Abstract:** Coromandel Marsh Dart Damselfly *Ceriagrion coromandelianum* (Fabricius) breeds in stagnant pools, small garden tanks and ornamental cement ponds containing submerged and/or floating vegetation. Eggs were collected to observe two aspects of larval development: (1) The hatching rate of eggs deposited in different vegetation (*Nymphaea nouchali*, *Lemna paucicostata*, *Hydrilla verticillata*). Although *C. coromandelianum* prefers to oviposit in the broad leaves of *N. nouchali*, the highest rate of hatching was found in *H. verticillata* (95.8%) followed by *N. nouchali* (87.6%) and *L. paucicostata* (81.3%). Hatching commenced on Day 5 and was completed by Day 9. Maximum hatching (56%) was recorded on the sixth day of oviposition followed by the seventh day (20%) in all three substrates. (2) To document the process of hatching as follows: Around three minutes prior to hatching, the embryo exhibits cyclic pumping and pushing movements of the head (caused by the peristaltic movement of the mid- and hind- gut) of low intensity followed by high intensity and long pumping movements interspaced with smaller pulsating movements. Swelling of the head forces the apical chorion to split along the micropylar chute and like a lid, the apical tip topples over as a conical cap. This allows the prolarva to exit the egg. As it does so, it twists and the thorax swells breaking the prolarval sheath and releasing the first instar larva.

**Keywords:** Egg, hatching, *Hydrilla verticillata*, *Lemna paucicostata*, *Nymphaea nouchali*, Prolarva.

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**Author contributions:** PRV studied the hatching rate while NRT documented the hatching process. RJA set up the project and evaluated the findings.

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## INTRODUCTION

Female damselflies oviposit on floating plants (epiphytic) or inside plant tissue (endophytic). In endophytic species the choice of ovipositing material depends upon “the initial preference” (Waage 1987), which is a suitable place both for landing and easy deposition of eggs into plant tissue (Mokrushov & Frantsevich 1976; Waage 1987; Martens 1992, 1993, 1994, 2001). According to Mokrushov & Frantsevich (1976), the appearance, morphology and texture of the plant triggers the female to deposit eggs. Some species oviposit in a single or very few species of plant, while others, although perhaps exhibiting distinct preferences, oviposit in a wide variety of plants (Martens 1996). Some species not only show preferences in selecting plant species, but also in parts of plants used for oviposition (Martens 1992; Wildermuth 1993; Grunert 1995). Corbet (1999) summarized that infertility, desiccation, displacement (by flooding) and parasitoid infection are the major cause of egg mortality in Odonata; however, no substantial information is available on the survival and successful hatching of eggs depending upon the ovipositing material selected by the female. Hatching in Odonata depends upon levels of dissolved oxygen (Punzo 1988; Miller 1992), onset of light or darkness (Tennessen & Murray 1978), rainfall (Lempert 1988), pH (Hudson & Berrill 1986), fluctuation in incubation temperature and humidity (Pilon & Masseur 1984; Sawchyn & Gillott 1974; Gillooly & Dodson 2000; Koch 2015; Ichikawa et al. 2017; Mendonca et al. 2018).

A general account of the hatching event of an odonate egg was described for the first time by Pierre (1904) in the Zygoptera *Lestes virides* (now *Chalcolestes viridis*). Later Tillyard (1916) documented this in the Aeshnidae *Anax papuensis*. Degrange (1961, 1974) studied the egg hatching of *Agrion puella*, *Enallagma cyathigerum* and *Calopteryx virgo* and reported that the endochorion has a pre-existing line of weakness which cracks when the prolarva hatches. He also reported that the micropyle orifices permit the entry of water during hatching.

*C. coromandelianum* is one of the most common Zygoptera in the Indian subcontinent. It breeds in stagnant pools and small garden tanks, tubs and ornamental cement ponds containing submerged and/or floating vegetation. In continuation of the study on the breeding biology of this species in central India (Andrew et al. 2011; Thaokar et al. 2018a,b), this communication evaluates the variation in the rate of hatching success in different oviposition substrates (*N. nouchali*, *L. paucicostata*, *H. verticillata*) and also describes the

behaviour of the embryo and events leading to hatching of the egg.

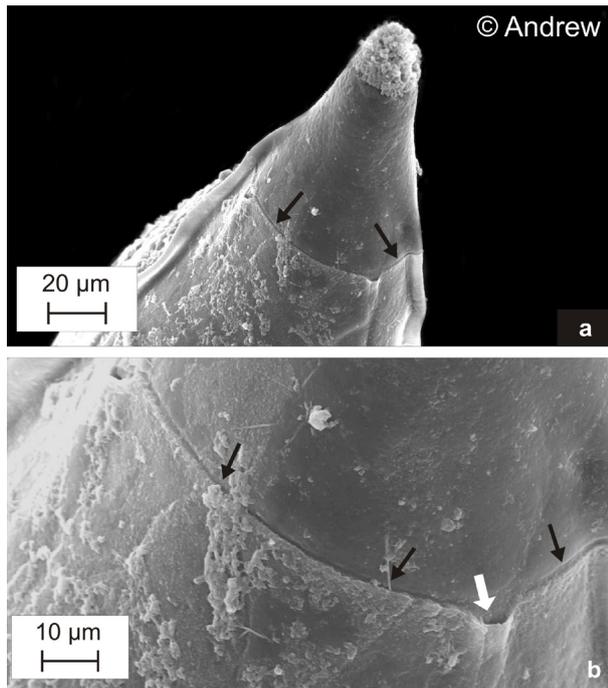
## MATERIAL AND METHODS

Leaves of *Nymphaea nouchali*, *Lemna paucicostata* and stems of *Hydrilla verticillata* bearing eggs of *Ceriagrion coromandelianum* were collected from 1000 h to 1400 h during the third week of February 2015 (Average temp. 34.2 °C (min. 31 °C, max. 36 °C); average humidity 51.4 % (min. 43, max. 66)) from small underground cement tubs at the botanical garden of Hislop College, Nagpur (21°8'51.43"N & 79°4'17.26"E), India. This site is being used to study the breeding and reproductive behaviour of *C. coromandelianum* details of which can be found in Andrew et al. (2011) and Thaokar et al. (2018a,b, 2019).

The samples were brought to the laboratory within two/three hours post oviposition, segregated and carefully cut into smaller pieces (without damaging the eggs). They were then labelled and placed in water from the collecting site in petri dishes to permit observation using binocular microscopes (Primo Star DV-4 and Magnus- MS 24). The water was replaced daily. The number of eggs in each piece of substrate of each petri dish was counted and constantly monitored for the following 15 days. The record of daily hatching was noted up to 1700 h each day and the final count of eggs hatched was tallied on the 10<sup>th</sup> day (the eggs were observed for the next five days in case of any late hatching). The process of egg hatching was photo/video-graphed with the help of aim-n-shoot Sony (DSC-W30) and Canon (G11) cameras. Detail of the weather reports for the region were obtained from the website <https://www.timeanddate.com>.

## OBSERVATION

The egg of *C. coromandelianum* is typically endophytic, with an elongate cylindrical shape (980 X 140 µm) bearing a pointed anterior and rounded posterior end. The pointed anterior end or the micropylar region (pedicle) is demarcated by a circular grooved line of hatching on the exochorion, which bears five micropylar orifices (Image 1) at regular intervals (Andrew et al. 2011). The micropylar region is apically brown up to (40 µm) while the remaining area is transparent or opaque. Below this region lies a ring of thicker endochorion, which stops the prolarva from moving upwards. The tip



**Image 1.** *Ceriagrion coromandelianum* – scanning electron micrograph of the apical tip of egg: a, b—showing the circular grooved line of hatching (black arrows) and the micropylar orifice (white arrows) (Andrew et al. 2011).

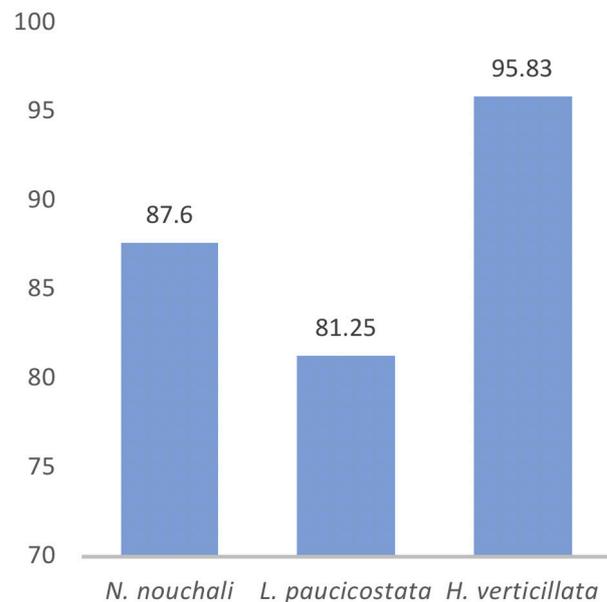
of the egg is covered with a thick tuft of aquatic debris. The embryo comes to lie just below the micropylar region and is housed below the chorionic rim while the micropylar lumen is empty. At this stage, the embryo is well-formed with a rounded head bearing a pair of conspicuous compound eyes as dark black spots. The thoracic segments cannot be demarcated but abdominal segments are slightly distinct. The process of hatching in *C. coromandelianum* initiates  $48 \pm 5$  minutes before emergence by a corresponding increase in the movement of the embryo, but active movement of the embryo starts about three minutes before the prolarva escapes from the egg.

#### i) The hatching rate of eggs deposited in different vegetation

*Ceriagrion coromandelianum* exhibits a hierarchy of preferences for oviposition and chooses floating leaves of *Nymphaea nouchali* over *Lemna paucicostata* and submerged *Hydrilla verticillata* (Thaokar et al. 2018a). Although *Ceriagrion coromandelianum* prefers to oviposit in the broad leaves of *Nymphaea nouchali*, the highest rate of hatching was found in the stems of *Hydrilla verticillata* (95.83%;SD 2.75, SE 1.59) followed by *N. nouchali* (87.60%; SD 1.63, SE 0.94), and *Lemna*

**Table 1.** Hatching details of *Ceriagrion coromandelianum* eggs by number of samples.

Vegetation	Number of eggs present	Number of eggs hatched	Hatching percentage
<i>Nymphaea nouchali</i>	88	78	88.63
	60	51	85.00
	102	90	88.23
<b>Total</b>	<b>250</b>	<b>219</b>	<b>87.60</b>
<i>Lemna paucicostata</i>	30	24	80.00
	36	30	83.33
	30	24	80.00
<b>Total</b>	<b>96</b>	<b>78</b>	<b>81.25</b>
<i>Hydrilla verticillata</i>	30	28	93.33
	18	18	100.00
	24	23	95.83
<b>Total</b>	<b>72</b>	<b>69</b>	<b>95.83</b>

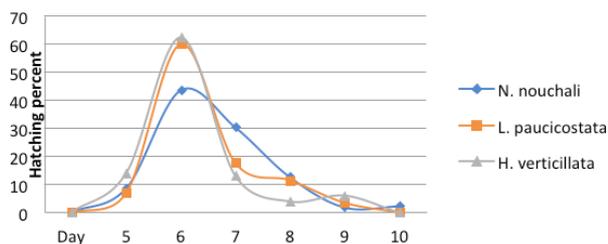


**Figure 1.** Hatching rate of *Ceriagrion coromandelianum* eggs in all samples.

*paucicostata* (81.25%; SD 1.57, SE 0.91) (Table 1, Figure 1). The Student's t-test indicates that there is a significant difference (at  $p = 0.05$ ) for hatching percentage between *N. nouchali* and *H. verticillata* (3.7808) and between *L. paucicostata* and *H. verticillata* (4.671). Hatching commenced from the fifth day (10%) post oviposition; however, maximum hatching (55.53%) was noticed on the sixth day followed by the seventh day (20.43%) in all three substrates. The process continued up to ninth day in *H. verticillata* and *L. paucicostata* and up to the 10<sup>th</sup> day in *N. nouchali* (Table 2, Figure 2).

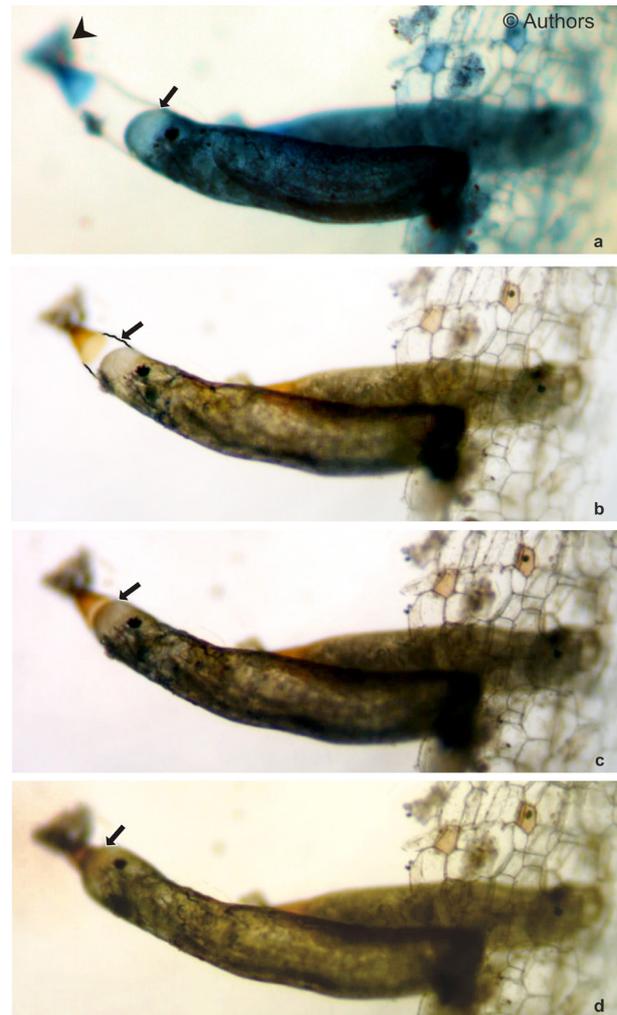
**Table 2.** Hatching details of *Ceriagrion coromandelianum* eggs by day number (Day 5 first day of emergence).

Day	<i>Nymphaea nouchali</i>	<i>Lemna paucicostata</i>	<i>Hydrilla verticillata</i>	Percentage
5	27	08	14	10.03
6	135	68	72	55.53
7	94	20	15	20.43
8	39	13	05	9.4
9	06	04	07	3.83
10	07	00	00	0.78

**Figure 2.** Hatching details of *Ceriagrion coromandelianum* eggs by day number.**ii) The process of hatching**

This is initiated with constant convulsive pumping movements of the head. Initially, this movement is of low intensity as the head moves to and fro just below the endochorionic ring. At this stage there is a total of  $42 \pm 8$  ( $N = 5$ ) movements which take 90–115 seconds. These head movements are caused by the peristaltic action of the mid- and hind gut. Hereafter, there is a change in the pumping intensity with 11–15 high pumping cycles alternating with low pumping movements. This continues for 22–36 seconds. These movements bring the head up to the endochorionic ring. After a pause of 8–15 seconds, the pumping movement recommences. At this stage the head pushes upwards with 14–20 long pumping movements interspaced with 3–7 smaller pulses (Image 2). This post-pause cycle of movement takes 18–37 seconds. The head now glides upwards and comes to occupy the complete micropylar region. With a strong final peristaltic motion, the head pushes on the apical tip of the egg. The pressure on the apical tip is further increased by the swelling of the head, which forces the apical chorion to split in a circular manner (along the micropylar chute) and the apical tip (brown area) topples over as a conical cap and the prolarva glides swiftly and easily out of the egg (Image 3).

The prolarva is enveloped by a fine chitinous envelope, 'the pro-larval sheath'. As the prolarva

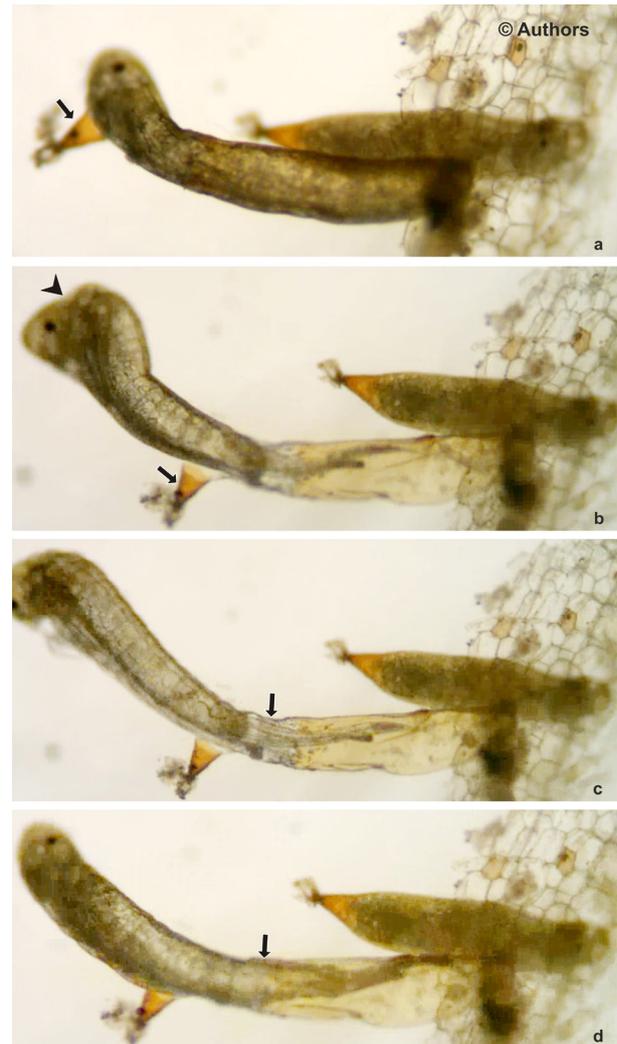
**Image 2.** *Ceriagrion coromandelianum* – serial photographs of hatching showing movement of the prolarva in the apical conical tip in the egg (arrows). Note the sticky egg tip covered with a tuft of debris (arrowhead).

escapes from the egg, the body twists sideways and the thorax swells breaking the pro-larval sheath anteriorly. This allows the first instar larva to emerge. Whilst the pro larval sheath remains stuck to the fractured edge of the eggshell. The first instar larva wriggles four to six times twisting its body before resting with spread legs and anal cerci. The head is held above the ground with the well-formed mask tucked beneath. The head and compound eyes are prominent, but ocelli are wanting. The body is transparent, devoid of midgut yolk, and a network of tracheoles can easily be traced (Image 4).

## DISCUSSION

In *Ceriagrion coromandelianum* completion of embryonic development and hatching are not separated by an interval as found in some odonates (Miller 1992) and therefore most eggs hatch within seven days. Hatching can be triggered by temperature, hypoxia, onset of light/darkness and rainfall. The minimum duration of direct hatching in most non hibernating species (like *C. coromandelianum*) varies from 5–7 days (Corbet 1999). *C. coromandelianum* often oviposits in temporary small ponds and there is strong selection pressure to complete the aquatic phase of the life cycle rapidly. It, therefore, not only exhibits a short hatching period but also rapid larval development within 35 days (Kumar 1980). Although low temperature, desiccation and flooding (Sawchyn & Gillott 1974; Duffy 1994; Bennett & Mill 1995) cause heavy mortality in odonate eggs, such conditions were not observed during the present study.

Egg clutches deposited in submerged vegetative substrate have a higher rate of hatching than those placed along the under-surface of floating vegetation. Many zygopterans exhibit underwater oviposition where the females walk down and lay eggs in submerged vegetation. Some genera descend up to 1 meter and can remain underwater for up to 2.5 hours (Corbet 1999). This high risk underwater oviposition gives free access to the oviposition site (Alcock 1987) and removal of male interference (Waage 1984). Further, when eggs are laid inside completely submerged vegetation, it decreases the risk of desiccation (Corbet 1999) and, as indicated from the present study, increases the rate of hatchability. In Odonata, the head of the embryo produces convulsive pumping movements before hatching. Although Tillyard (1916) believed that this action is caused by a special hatching organ the ‘cephalic heart’, it is now well established that swallowing of the amniotic fluid by the embryo causes these movements (Grieve 1937; Wolfe 1953; Corbet 1965, 1999). As we have observed, in *C. coromandelianum*, the head of the prolarva produces cyclic movements which synchronize with the peristaltic movement of the gut, probably caused by the intake of amniotic fluid by the embryo. In *Anax papuensis* (Tillyard 1916), the head lies just below the anterior end of the eggshell i.e. the micropylar apparatus; however, in *Epiophlebia superstes*, the head is lodged inside the lumen of the pedicel and this region contains the micropylar apparatus (Sahlén 1994; Andrew & Tembhare 1997). In *C. coromandelianum* the head is located below the pedicel and is demarcated by the chorionic ring. The



**Image 3.** *Ceriagrion coromandelianum* – serial photographs of hatching showing breaking of the apical tip of the egg (a & b arrows) followed by swelling of the head (b-arrowhead) and twisting of the prolarva to escape from the prolarval sheath (c & d arrows).

embryo head of *C. coromandelianum* initially passes through the chorionic ring and comes to lie in the lumen of the pedicel, where it commences butting the pedicel with stronger pumping movements and swelling of the head. Similar movements are probably undertaken by the embryo of many odonates before hatching (Corbet 1999).

In dragonflies exhibiting exophytic oviposition, the eggs are mostly spherical and the embryo does not exert a localised upward pressure as found in the endophytic egg. The embryo circulates inside the egg in a spiral manner just before hatching and forms a vertical slit to escape from the egg (Miller 1995). In *C. coromandelianum* the embryo pushes and exerts pressure on the apical pedicel which weakens along the



**Image 4.** *Ceriatrion coromandelianum* – serial photographs of hatching showing emergence of the first instar larva (arrows) by shedding the prolarva sheath (PLS) which is held by the fractured edge of the eggshell.

rim of micropylar chute around the pedicel of the egg (Andrew et al. 2011). This ‘pre-existing line of weakness’ (Degrange 1961, 1974) of the egg breaks and the pedicel topples off like a lid. In *Anax papunesis* (Tillyard 1916), *Enallagma cyathigerum*, *Calopteryx virgo* (Degrange 1961, 1974) and *Anax guttatus* (Andrew & Tembhare 1997), the endophytic egg exhibits both conditions, as the embryo escapes from the egg, the pedicel not only pops out but a vertical slit is also produced, which gives ample space for the embryo to escape.

The duration of the prolarva stage depends upon the ease with which it can free itself from the jelly or detritus around the egg, and also upon the distance it must travel to reach water (Asahina 1950; Robert 1958; Corbet 1999). The duration of the prolarval stage varies from less than a minute as found in *Anax papunesis* (Tillyard 1916) *Brachydiplax sobrina* (Chawdhury &

Chakraborty 1988); *Ictinogomphus rapax*, *Rhodothemis rufa* (Begum et al. 1980, 1990), 40 minutes in *Zygonia petiolatum* (Begum et al. 1982) and about four hours in *Epiophlebia superstes* and *Epitheca bimaculata* (Robert 1958). In *C. coromandelianum* the prolarval stage is almost non-existent because the prolarva does not have to free itself from jelly or aquatic detritus (since the detritus is restricted to the projecting pedicel tip, which detaches during hatching) and the prolarva does not have to travel to find suitable habitat (Thaokar et al. 2018a). In summary, the prolarva discards the prolarval sheath as it leaves the egg allowing the first instar larva to escape. The yolk material as found in the gut of the first instar larva of *Anax papunesis* (Tillyard 1916) is not found in *C. coromandelianum* probably because of its very short prolarval stage and as it emerges from the egg fully equipped with functional mouthparts.

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### Notes

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